Effects of Irrigation, Sulfur, and Fumigation on Streptomyces Soil Rot and Yield Components in Sweetpotato

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We are grateful to C. Clark, J. Moyer, and W. Jester III for discussions and assistance on aspects of this research. The technical assistance of G. Parra, M. Hord, and A. Schepps is appreciated. The statistical assistance of M. Gumpertz is appreciated.
This work was funded in part by the North Carolina Agricultural Research Service and in part by the North Carolina Sweetpotato Commission.
Accepted for publication 23 March 1992.

ABSTRACT

Ristaino, J. B., and Averre, C. W. 1992. Effects of irrigation, sulfur, and fumigation on Streptomyces soil rot and yield components in sweetpotato. Phytopathology 82:670-676.

The effect of fibrous root infection by *Streptomyces ipomoea* on disease on storage roots and production of marketable yield in the susceptible sweetpotato cultivar Jewel was evaluated in replicated field studies conducted over 3 yr. Levels of disease were manipulated by soil treatments with drip irrigation (main plots), reduction of soil pH with sulfur (subplots), and soil fumigation with Telone C-17 (sub-subplots). Sweetpotatoes were grown in a field with natural inoculum of *S. ipomoea* in 1 yr or were artificially infested in other years. Irrigation reduced disease on fibrous roots to the greatest extent in plots not treated with sulfur or fumigated and increased the number of storage roots produced per plant in all years. Irrigation reduced the number of diseased storage roots produced per plant in the low rainfall year of 1990 but did not significantly increase yields in any year. Although addition of sulfur reduced the severity of the disease on fibrous roots in nonfumigated plots in 1988 and 1990, it also reduced yields by 21–33% in 2 of 3 yr because fewer storage roots were produced per plant in sulfur-treated plots. Fumigation reduced the percentage of diseased storage roots produced per plot from 71, 8, and 22% in nonfumigated plots to 52, 3, and 6% in fumigated plots in 1988, 1989, and 1990, respectively. Fumigation also reduced the number of diseased storage roots produced per plant and the severity of disease on fibrous roots in each year. Only fumigation increased the yield of marketable storage roots by 68 and 19% in 2 of 3 yr. Path analysis demonstrated that the severity of disease on fibrous roots had an important direct effect on marketable yield and important indirect effects on marketable yield by affecting the percentage of diseased storage roots produced per plot, the number of diseased storage roots per plant, and the number of storage roots per plant. The severity of disease on fibrous roots was positively correlated with the percentage of diseased storage roots produced per plot ($r = 0.84$) and the number of diseased storage roots produced per plant ($r = 0.64$), and the severity of disease on fibrous roots was negatively correlated with the number of storage roots produced per plant ($r = -0.66$). Yield of marketable storage roots was negatively correlated with both the severity of disease on fibrous roots ($r = -0.77$) and the percentage of diseased storage roots produced per plot ($r = -0.73$). These data demonstrate the importance of fibrous root disease in this pathosystem. Management strategies that reduce disease on fibrous roots may ultimately lead to increased yield of storage roots.

Additional keywords: actinomycete, *Ipomoea batatas,* pox.

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is a major vegetable crop in North Carolina with over 30,000 acres produced. Streptomyces soil rot or pox, caused by the actinomycete *Streptomyces ipomoea,* is a destructive root disease of sweetpotato. Necrotic lesions develop on fibrous roots leading to root rot, and scablike lesions develop on storage roots that reduce the marketability of the crop (6,28). Severe infections cause yield loss through suppressed production or malformation of roots (17). Although resistant cultivars are available (11,20,24,34,35), the disease continues to cause losses in North Carolina where the susceptible cultivar Jewel is extensively grown. Management of the disease involves the use of integrated approaches, including soil fumigation, crop rotation, and reduction of soil pH with sulfur. The implementation of more efficient management strategies for Streptomyces soil rot requires more specific knowledge of the effect of disease on yield components.

The sweetpotato plant produces a complex root system that consists primarily of fibrous roots and storage roots (13). Although these root types differ physiologically and morphologically, both are susceptible to the pathogen (6,13). The effect of fibrous root infection by *S. ipomoea* on disease development on storage roots and yield in the field has not been quantified previously. Because infections on storage roots originate from infected secondary fibrous roots, factors that reduce disease on fibrous roots may reduce disease on storage roots and improve yield (6).

Considerable research has been conducted on the use of chemicals for control of Streptomyces soil rot (2,7,17,18,21,22), but few studies have attempted to compare chemical control with cultural practices (17). Preplant treatment with soil fumigants containing chloropicrin can reduce disease on storage roots and increase marketable yield (2,7,17,22). However, effects of fumigation on disease on fibrous roots and specific yield components of sweetpotato have not been fully described. Susceptible sweetpotato cultivars can be grown in infested fields with minimal disease if the soil pH is reduced below 5.2 by addition of sulfur (12,23,24,30). Disease development can be severe when pH is increased with lime (12,23,24). Sweetpotatoes generally grow better and produce a greater yield at soil pH levels ranging from 6.0 to 6.5 (9).

An early study on Streptomyces soil rot indicated a negative correlation between the level of soil moisture and disease (31). Less disease occurred under saturated soil conditions than when soil was allowed to dry to a soil water content of 2–5% (31). Others have noted the relationship between dry soil and disease development (19,26–28,30), but no published research has evaluated the effects of irrigation on the development of Streptomyces soil rot on sweetpotato in the field. In England and elsewhere, common scab of Irish potato caused by *S. scabies* has been effectively controlled through the use of irrigation (14–16). The potential exists to manipulate soil moisture by irrigation and to reduce disease caused by *S. ipomoea* on sweetpotato.

The objective of this work was to evaluate the effects of irrigation, sulfur, and soil fumigation on the infection of sweetpotato fibrous roots and storage roots by *S. ipomoea.* In addition, the effects of fibrous root infection on development of disease on storage roots and on components of yield in the field was evaluated with path coefficient analysis. A portion of this research has been published (32,33).

MATERIALS AND METHODS

Inoculum preparation. Stock cultures of *S. ipomoea* were maintained on silica gel at 5 C (36). An isolate of *S. ipomoea,* number 78-57, pathogenic to sweetpotato and originally isolated from North Carolina was obtained from C. Clark, Louisiana State University, and used to infest field plots in 1989 and 1990. Cultures were grown on *Streptomyces* growth medium (20 g of mannitol, 0.2 g of K_2HPO_4, 0.2 g of $MgSO_4 \cdot 7H_2O$, 5.0 g of NaCl, 2.0 g of $CaCO_3$, 0.2 mg of $CoCl_2$, 1.0 g of yeast extract, 18.0 g of agar, and 1.0 L of distilled water) at 32 C for 8–10 days before transfer (5). Inoculum for use in field experiments was prepared by culturing the pathogen at 32 C for 4 wk in 500 cm^3 of vermiculite and 375 ml of broth (5.0 g of mannitol, 1.0 g of sodium proprionate, 0.2 g of K_2HPO_4, 0.2 g of $MgSO_4 \cdot 7H_2O$, 1.0 g of yeast extract, 2.0 g of $CaCO_3$, 0.11 mg of $CoCl_2$, and 1.0 L of distilled water) contained in 1.0-L mason jars. Inoculum consisted of aerial mycelia and spores of the pathogen in a vermiculite carrier.

Field experiments. Sweetpotatoes were grown using recommended cultural practices (40). To produce transplants for use in the field, storage roots of the cultivar Jewel were dipped in Mertect 340 F at the labeled rate of 8.36 ml/L of water (0.46 kg/L a.i., Merck and Co., Rahway, NJ) and planted in beds in early April. The beds were previously fumigated with methyl bromide-chloropicrin (MB-33, 3.6 kg/83.6 m^2, Great Lakes Chemical Co., West Lafayette, IN). After the roots were planted, beds were covered with clear 1-mil polyethylene (0.025 mm thick) that was punctured for ventilation. The polyethylene was removed after plant emergence.

Experiments were conducted on sandy loam soils in all years. In 1988, a grower's field located in Pender County, NC, was used, whereas in 1989 and 1990 fields were located at the Central Crops Research Station in Clayton, NC. The field in Clayton was fumigated with methyl bromide-chloropicrin (MB-33, 3.6 kg/83.6 m^2) in the spring before planting. In 1988 and 1989, plots were 9.1 m long, and in 1990 plots were 12.2 m long and consisted of two single-row beds that were each 1.1 m wide. Within-row spacing was 30.5 cm. The experiment was arranged in a split-split-plot design, with a factorial arrangement of treatments applied at two levels (present or absent). Drip irrigation was applied to main plots, sulfur to subplots, and soil fumigant (Telone C-17, 85% 1,3-dichloropropene, 16.5% chloropicrin, Dow Chemical Co., Midland, MI) to sub-subplots. Treatments were replicated four times.

Plots at the grower's field in 1988 contained natural inoculum of the pathogen, whereas plots in 1989 and 1990 were artificially infested with inoculum of *S. ipomoea* at a rate of 212 cm^3 per meter of row. A furrow was dug in the center of each row and inoculum was buried approximately 10 cm below the soil surface. Beds were reshaped with a disk hiller after infestation. Plots were infested approximately 2–3 wk before planting.

Soil in appropriate subplots was either not treated or treated with sulfur (90% a.i., Chemical Works, Inc., Fort Valley, GA) before fumigation. Sulfur was applied at rates of 373, 452, or 519 kg/ha in 1988, 1989, and 1990, respectively, to lower soil pH to 5.2. Sulfur was mixed with water in a watering can and banded on the soil surface. Plots were cultivated to mix the sulfur in the row. Levels of sulfur applied to subplots varied among years because initial mean soil pH varied. Rates were calculated on the basis of formulas provided by the North Carolina Department of Agriculture's Soil Testing Service (37). Lime was applied to individual subplots not treated with sulfur in 1989 and 1990 (1,383 and 1,553 kg/ha) to raise soil pH above 6.0, whereas the entire field was limed before planting in 1988.

Soil in appropriate sub-subplots was fumigated with Telone C-17 on the same day that plots were infested with the pathogen. The fumigant was applied by chisel injection approximately 20 cm below the soil surface at the labeled rate of 310.5 ml per 30.5 m of row, and then soil was applied over the top of the row with the disk hiller.

Sweetpotato sprouts 20 cm in length were cut from the plant beds in June (8 wk after beds were planted) and transplanted into plots 2–3 wk after soil fumigation. Untreated border plots, the same size as treated plots, also were planted. All plots were irrigated immediately after transplanting with overhead irrigation to establish plants. Subsequently, main plots either were not irrigated or irrigated with a drip system (Chapin Twin-wall IV, Chapin Watermatics, Inc., Watertown, NY). A single, drip-irrigation line with emitters spaced 30.5 cm apart was buried 10 cm below the soil surface and approximately 10 cm from one side of the plant row in each irrigated plot. Main plots were drip-irrigated for a 4-h duration approximately three times per week. Plots were not irrigated on days when rainfall occurred. Water was applied at a rate of 1.9 L/min per 30.5 m of row at a pressure of 68.9 kPa.

Data collection. Five soil cores (1.9 cm in diameter × 20 cm in depth) were sampled from each plot before soil treatment with sulfur and at two times during the season to measure soil pH at each location. The top 5 cm of soil from each core was discarded, and cores from each plot were combined into a composite sample for soil pH. Standard methods were used to measure soil pH (25).

Rainfall during the season was recorded with a rain gauge at the field location in 1989 and 1990 and at a nearby (16 km) experiment station in 1988. Soil water content was not measured in the grower's field in 1988. Soil water content at 20-cm depths was measured five times during the season in all plots in 1989 by gravimetric methods. In 1990, a neutron probe (Troxler Scientific Instruments, Research Triangle Park, NC) was used to take measurement counts at 20-cm depths three times during the season. Measurement counts were converted to volumetric water content using a calibration equation developed for the field. Soil water content is expressed on a volumetric basis.

Five to eight plants were randomly sampled at harvest from one of the two rows in each experimental unit. Roots were dug to a 30-cm depth below each sampled plant. The severity of disease was evaluated visually on fibrous roots of individually sampled plants and rated using a scale of 0 to 4, where 0 = no lesions, 1 = <25% of the fibrous root system with lesions, 2 = 26–50% of the fibrous root system with lesions, 3 = 51–75% of the fibrous root system with lesions, and 4 = >75% of the fibrous root system with lesions. The total number of storage roots and diseased storage roots, and the dry weight of fibrous roots, storage roots, and shoots (vines and leaves), were measured on each sampled plant. Weights were determined after drying tissue at 60 C in an oven for approximately 1 wk. Storage roots were sliced to facilitate drying.

Yield was measured in the second row of each experimental unit. Total yield (U.S. #1s, jumbos, and canners), yield of marketable storage roots (free of lesions), and yield of diseased storage roots were determined by measuring fresh weight. The percentage by weight of the total yield of storage roots affected by disease was calculated.

Statistical analysis. Separate analyses of variance were conducted for data from each year with the Statistical Analysis System (SAS Institute, Cary, NC). Before analysis of variance, data were tested for homogeneity of variance by observing scatter plots of residuals. Variances were found to be similar for all 3 yr and, consequently, data from the 3 yr were combined. An analysis was performed with year in the model as the main plot, irrigation as the subplot, sulfur as the sub-subplot, and fumigation as the sub-sub-subplot. In cases where treatment effects differed from year to year (significant treatment × year interactions in Table 1), means from the highest order interactions were discussed separately for each year. Otherwise, means were combined for the 3 yr. Repeated measures analyses of variance were conducted on soil pH data and volumetric soil water content data collected over time separately for each year.

Simple correlation coefficients were calculated between pairs of measured variables collected over 3 yr. Path coefficient analysis was used to decompose and interpret the linear relationship among measured variables (8,38,41). Significant correlation coefficients were partitioned into direct effects using standardized partial

TABLE 1. Sources of variation and P values for effects of year, drip irrigation, soil treatment with sulfur, and fumigation with Telone C-17 on disease caused by *Streptomyces ipomoea* and yield components in sweetpotato cultivar Jewel

Source of variation	Degrees of freedom	$P > F$ values: Severity of disease on fibrous roots	Percentage of diseased storage roots per plot	Number of diseased storage roots per plant	Marketable yield[a]	Number of storage roots per plant
Year[b]	2	0.01*[c]	0.01*	0.01*	0.01*	0.01*
Block × year	9					
Irrigation[d]	1	0.31	0.38	0.09	0.19	0.05*
Irrigation × year	2	0.91	0.49	0.02*	0.31	0.37
Block (irrigation × year)	9					
Sulfur[e]	1	0.05*	0.29	0.42	0.01*	0.03*
Sulfur × year	2	0.05*	0.38	0.20	0.01*	0.07
Irrigation × sulfur	1	0.08	0.30	0.09	0.94	0.38
Irrigation × sulfur × year	2	0.18	0.56	0.85	0.96	0.57
Block (irrigation × sulfur × year)	18					
Fumigation[f]	1	0.01*	0.01*	0.01*	0.01*	0.01*
Fumigation × year	2	0.04*	0.01*	0.01*	0.82	0.05*
Irrigation × fumigation	1	0.97	0.22	0.06	0.56	0.92
Irrigation × fumigation × year	2	0.54	0.85	0.76	0.91	0.14
Sulfur × fumigation	1	0.19	0.85	0.73	0.31	0.31
Sulfur × fumigation × year	2	0.01*	0.48	0.01*	0.04*	0.76
Irrigation × sulfur × fumigation	1	0.04*	0.85	0.07	0.08	0.20
Irrigation × sulfur × fumigation × year	2	0.17	0.55	0.36	0.46	0.54

[a] Measured in kilograms per plot.
[b] The effect of year was tested using block × year as an error term.
[c] *, $P > F$ value significant at the 0.05 level or lower.
[d] Drip irrigation applied to main plots for 4 h three times per week. Irrigation main effect and irrigation × year interaction term tested using block (irrigation × year) as an error term in the analysis.
[e] Sulfur was applied to soil at a rate of 373 or 519 kg/ha in 1988 and 1990, respectively. Sulfur main effect and the other sulfur × irrigation × year interaction terms were tested using block (irrigation × sulfur × year) as an error term in the analysis.
[f] Telone C-17 was applied by chisel injection approximately 30 cm below the soil surface at the labeled rate of 310.5 ml per 30.5 m of row. The fumigation main effect and the remaining interaction terms were tested using the residual as an error term in the analysis.

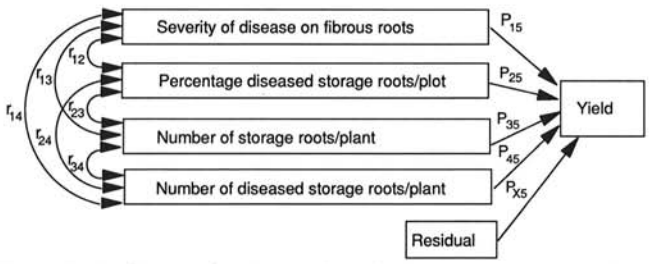

Fig. 1. Path diagram for the relationship between measured variables and marketable yield of storage roots of sweetpotato cultivar Jewel over 3 yr. Significant correlation coefficients were partitioned into direct effects using path coefficients (P_{ij}) and indirect effects (path coefficients × correlation coefficients [r_{ij}]).

regression coefficients (path coefficient) and indirect effects (path coefficient × correlation coefficient) for each measured variable. Path analysis was conducted to determine the relationship between yield of marketable storage roots (dependent variable) and four independent variables, including the severity of disease on fibrous roots, the percentage of diseased storage roots per plot, the number of storage roots per plant, and the number of diseased storage roots per plant (Fig. 1).

RESULTS

Soil pH and moisture. Soil pH changed over time in each year (time effect significant each year at $P = 0.01$). Soil pH values before planting were 6.0, 5.7, and 6.3 in 1988, 1989, and 1990, respectively (Table 2). In 1988, soil pH was significantly lower in sulfur-treated plots at the time of the second measurement (41 days after planting), but pH increased and did not differ from limed plots by the last measurement time (Table 2). In contrast, soil pH over time was significantly affected by sulfur in 1989 and 1990 ($P < 0.01$ for each year), and soil pH was significantly lower at the last measurement time in plots treated with sulfur (Table 2).

TABLE 2. Effect of soil treatment with sulfur or lime on soil pH values over time from experiments conducted in 1988, 1989, and 1990

Treatment and year	Time 1[a]	Time 2	Time 3
1988			
Sulfur[b]	6.0[c]	5.2	5.6
Lime	6.0	5.7	6.0
1989			
Sulfur[b]	5.7[c]	4.6	4.6
Lime	5.7	4.6	6.2
1900			
Sulfur[b]	6.3[c]	5.4	4.4
Lime	6.3	5.8	5.0

[a] Soil pH values were measured at time 1 (before application of sulfur), at time 2 (41, 34, and 37 days after planting in 1988, 1989, and 1990, respectively), and at time 3 (84, 55, and 124 days after planting in 1988, 1989, and 1990, respectively) at each field.
[b] Sulfur was applied to soil in a water slurry and cultivated into the beds at a rate of 373, 452, or 519 kg/ha in 1988, 1989, and 1990, respectively.
[c] Soil pH was significantly lower at time 2 but not significantly different over time in sulfur-treated and lime-treated plots in 1988 ($P = 0.04$). Soil pH was significantly different over time between plots treated with sulfur and lime in 1989 and 1990 (sulfur × time effect significant at $P < 0.01$).

Less total rainfall occurred between the time of planting and harvest at the field location in 1990 (41 cm) than in 1988 (68.2 cm) and 1989 (63 cm). Soil water contents over time at 20-cm depths were significantly affected by irrigation in 1989 and 1990 (time × irrigation interaction significant at $P < 0.01$ and 0.05 for 1989 and 1990, respectively). Mean volumetric soil water

contents ranged from 17.5 to 22.0% in irrigated plots and from 12.5 to 20.0% in nonirrigated plots during the season in 1989, whereas mean volumetric soil water contents ranged from 15.7 to 18.1% in irrigated plots and from 10.25 to 14.4% in nonirrigated plots during the season in 1990. Soil water content was not monitored at the grower's field in 1988.

Disease on storage and fibrous roots. Irrigation reduced disease on fibrous roots to the greatest extent in plots that were not fumigated or treated with sulfur in all years (irrigation × sulfur × fumigation interaction significant at $P = 0.04$) (Fig. 2A and Table 1). Similarly, sulfur reduced the severity of disease on fibrous roots to a greater extent in plots that were not fumigated or irrigated (Fig. 2A). Fumigation reduced the severity of disease on fibrous roots to a greater extent than either irrigation or sulfur alone (Fig. 2A). The response of fibrous root disease to sulfur and fumigation differed among years (sulfur × fumigation × year effect significant at $P = 0.01$) (Table 1 and Fig. 2B). Fibrous root disease was most severe in 1988, and sulfur reduced disease on fibrous roots in nonfumigated plots in 1988 and 1990, but not in 1989 because the level of fibrous root disease was lower in that year (Fig. 2B).

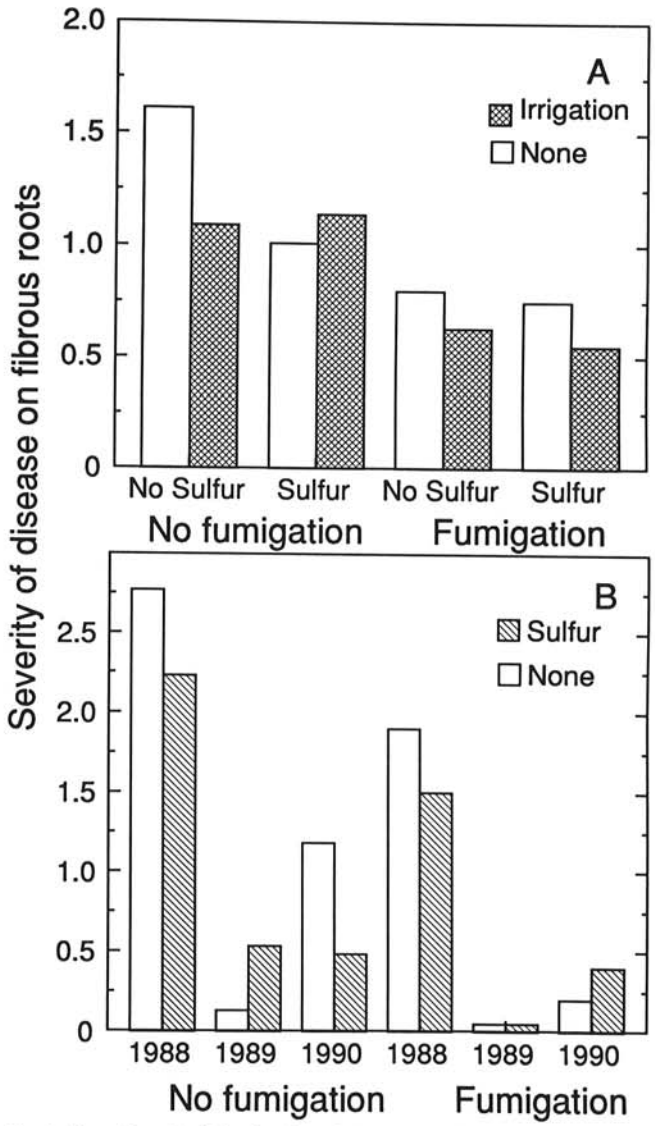

Fig. 2. The effect of soil fumigation with Telone C-17 and **A,** drip irrigation or soil treatment with sulfur on the severity of fibrous root disease caused by *Streptomyces ipomoea,* and **B,** soil treatment with sulfur on the severity of fibrous root disease caused by *S. ipomoea* in 1988, 1989, and 1990. Data shown in A are the irrigation × sulfur × fumigation means over 3 yr and $LSD_{0.05} = 0.16$ for comparisons between all treatments. Data shown in B are the sulfur × fumigation means for each year and $LSD_{0.05} = 0.58$, 0.28, and 0.47 in 1988, 1989, and 1990, respectively.

Fumigation significantly reduced the percentage of diseased storage roots produced per plot in each year, but the magnitude of the fumigation effect varied from year to year (fumigation × year significant at $P = 0.01$; Table 1 and Fig. 3). The percentage of diseased storage roots was greater in 1988 in fields with natural inoculum of the pathogen than in 1989 and 1990 in the artificially infested fields (Fig. 3). However, the percentage of diseased storage roots in the artificially infested plots in both 1989 and 1990 was sufficiently high to measure effects of fumigation on disease. The mean percentage of diseased storage roots per plot was 71, 8.2, and 22.3% in nonfumigated plots and 52.9, 2.7, and 5.9% in fumigated plots in 1988, 1989, and 1990, respectively (Fig. 3).

The effect of sulfur and fumigation on the number of diseased storage roots produced per plant also differed among years (sulfur × fumigation × year effect significant at $P = 0.01$; Table 1 and Fig. 4). Fumigation reduced the total number of diseased storage

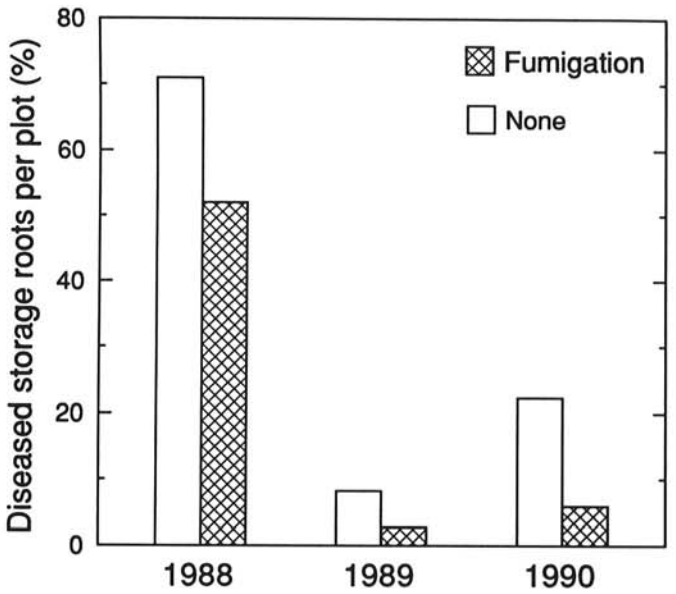

Fig. 3. The effect of fumigation with Telone C-17 on the percentage of diseased storage roots infected with *Streptomyces ipomoea* in 1988, 1989, and 1990. The fumigation main effect means are shown and were significant at $P = 0.01$ in each year.

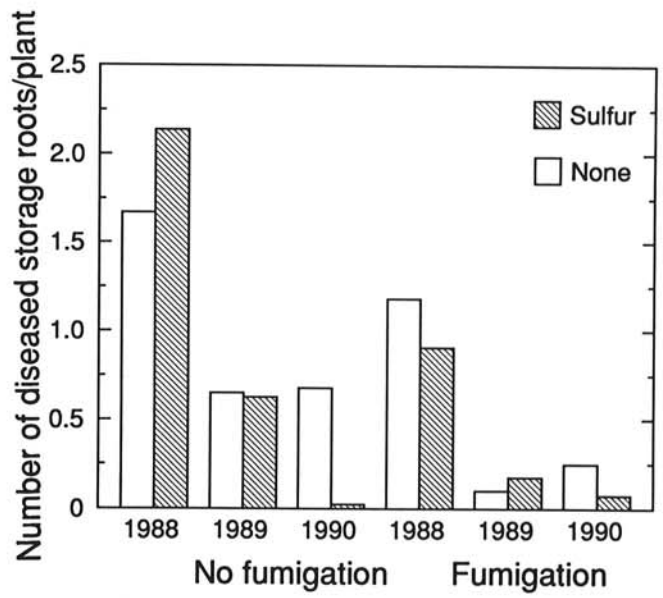

Fig. 4. The effect of soil treatment with sulfur on the number of diseased storage roots per plant in Telone C-17 fumigated or nonfumigated plots. Data shown are the sulfur × fumigation means for each year. $LSD_{0.05} = 0.9$, 0.4, and 0.2 in 1988, 1989, and 1990, respectively, for comparisons within years.

roots produced per plant in each year, whereas sulfur only reduced the number of diseased storage roots produced per plant in 1990 (Fig. 4). Irrigation also reduced the number of diseased storage roots produced per plant from 6.6 to 4.7 in 1990 (irrigation × year significant at $P = 0.02$; Table 1), but it had no effect in 1988 or 1989.

Disease effects on yield. Overall marketable yields of sweetpotato storage roots were lower in 1988 in the grower field, where disease incidence was high, than in 1989 and 1990 in the artificially infested plots (Fig. 5). Yield of marketable storage roots was negatively correlated with the severity of disease on fibrous roots ($r = -0.77$) (Fig. 5), the percentage of diseased storage roots produced per plot ($r = -0.73$) (Fig. 6), and the number of diseased storage roots produced per plant ($r = -0.51$) (Table 3). There was a high positive correlation between the severity of disease on fibrous roots and the percentage of diseased storage roots produced per plot ($r = 0.84$) (Table 3).

The effect of sulfur and fumigation on marketable yield differed among years (fumigation × sulfur × year interaction significant at $P = 0.04$) (Table 1 and Fig. 7). Fumigation of soil infested with *S. ipomoea* significantly increased the yield of marketable storage roots by 68% in 1988 and 19% in 1990, but the response to fumigation was dependent on sulfur treatment in 1990 (Fig. 7). Sulfur had a negative effect on marketable yield of storage roots in both 1989 and 1990, but sulfur did not affect yield in 1988 (Fig. 7). Sulfur reduced marketable yield by 33 and 7% in 1989 and by 21 and 27% in 1990 in nonfumigated or fumigated plots, respectively. Irrigation did not significantly affect marketable yield in any year.

Marketable yield was positively correlated with the number of storage roots produced per plant ($r = 0.72$) (Table 3). Fumigation increased the total number of storage roots produced per plant from 3.1 to 4.8 in 1988, but fumigation did not affect the number of storage roots produced per plant in 1989 or 1990 (fumigation × year interaction was significant at $P = 0.05$) (Table 1). Irrigation increased the mean number of storage roots produced per plant from 5.6 to 6.7 (irrigation effect significant at $P = 0.05$), and sulfur decreased the mean number of storage roots produced per plant from 6.5 to 5.7 (sulfur effect significant at $P = 0.03$) (Table 1) in all years.

Path analysis indicated that the most important path of influence of infection on marketable yield of storage roots was via the direct effect of disease on fibrous roots (Fig. 1 and Table 4). In addition, an equally important path of influence was the direct effect of the number of storage roots produced per plant on yield. However, the indirect effect of the severity of disease on fibrous roots was a large component of the total correlation between the number of storage roots produced per plant and yield (Table 4). The severity of disease on fibrous roots was negatively correlated with the number of storage roots produced per plant ($r = -0.66$) and positively correlated with the number of diseased storage roots produced per plant ($r = 0.64$) (Table 3). The indirect effects of the severity of disease on fibrous roots via the percentage of diseased storage roots produced per plot

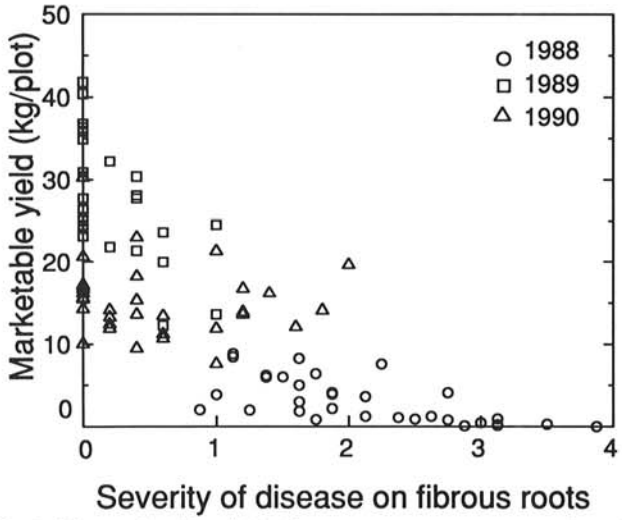

Fig. 5. The marketable yield of sweetpotato storage roots of cultivar Jewel plotted as a function of final severity of disease on fibrous roots (relative scale of 0 to 4). Data shown are individual plot means from experiments conducted in 1988, 1989, and 1990. $r = -0.77$ and was significant at $P = 0.001$.

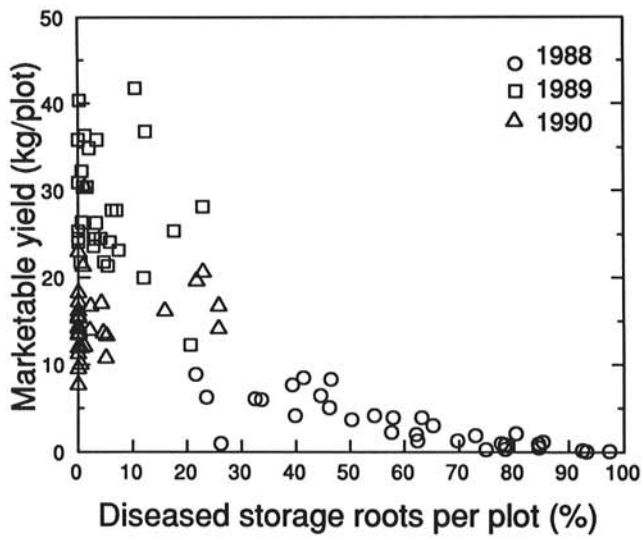

Fig. 6. The marketable yield of sweetpotato storage roots of cultivar Jewel plotted as a function of percentage of diseased storage roots. Data shown are individual plot means from experiments conducted in 1988, 1989, and 1990. $r = -0.73$ and was significant at $P = 0.001$.

TABLE 3. Linear correlation coefficients[a] between marketable yield of sweetpotato storage roots (cultivar Jewel), severity of disease on fibrous roots, percentage of diseased storage roots per plot, and the number of storage roots and diseased storage roots per plant from field data collected in 1988, 1989, and 1990

	Severity of disease on fibrous roots	Percentage of diseased storage roots per plot	Number of storage roots per plant	Number of diseased storage roots per plant
Marketable yield	−0.77	−0.73	0.72	−0.51
Severity of disease on fibrous roots		0.84	−0.66	0.64
Percentage of diseased storage roots per plot			−0.60	0.73
Number of storage roots per plant				−0.35

[a] All correlation coefficients significant at $P = 0.001$.

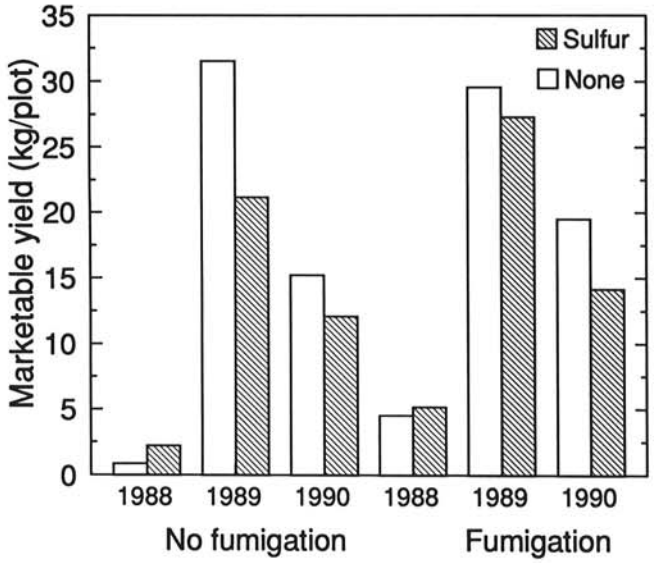

Fig. 7. The effect of soil treatment with sulfur on the yield of marketable storage roots of cultivar Jewel in plots that were not fumigated or fumigated in 1988, 1989, and 1990 with Telone C-17. Data shown are the sulfur × fumigation means for each year. $LSD_{0.05} = 1.31$, 6.47, and 5.81 in 1988, 1989, and 1990, respectively, for comparisons within years.

TABLE 4. Path coefficient analysis of the relationship between marketable yield of sweetpotato storage roots (cultivar Jewel) and the severity of disease on fibrous roots, the percentage of diseased storage roots per plot, and the number of storage roots and diseased storage roots per plant

Pathways of association	Coefficients
Severity of disease on fibrous roots vs. marketable yield	
Direct effect, P_{15}	−0.351[a]
Indirect effects[b]	
via percentage of diseased storage roots per plot	−0.199
via number of diseased storage roots per plant	0.007
via number of storage roots per plant	−0.228
Total correlation	−0.772[c]
Percentage of diseased storage roots per plot vs. marketable yield	
Direct effect, P_{25}	−0.239[a]
Indirect effects[b]	
via severity of disease on fibrous roots	−0.293
via number of diseased storage roots per plant	0.008
via number of storage roots per plant	−0.206
Total correlation	−0.730[c]
Number of storage roots per plant vs. marketable yield	
Direct effect, P_{35}	0.347[a]
Indirect effects[b]	
via severity of disease on fibrous roots	0.231
via percentage of diseased storage roots per plot	0.142
via number of diseased storage roots per plant	−0.004
Total correlation	0.716[c]
Number of diseased storage roots per plant vs. marketable yield	
Direct effect, P_{45}	0.011[a]
Indirect effects[b]	
via severity of disease on fibrous roots	−0.225
via percentage of diseased storage roots per plot	−0.174
via number of storage roots per plant	−0.122
Total correlation	−0.510[c]
Residual	0.56
Coefficient of determination	0.69

[a] Standardized partial regression coefficient (path coefficient).
[b] Path coefficient × correlation coefficient ($P_{ij} \times r_{ij}$).
[c] Correlation coefficients were significant at $P = 0.001$.

and the number of diseased storage roots produced per plant were also large components of the total correlation between these variables and marketable yield (Table 4).

Dry matter production. In 1988 and 1989, irrigation increased the dry weight of fibrous roots by 25–27% in fumigated plots but did not affect the dry weight of fibrous roots in plots that were not fumigated (fumigation × irrigation interaction significant at $P = 0.03$ in each year). Fumigation alone increased the dry weight of fibrous roots in 1990 ($P = 0.04$). Fumigation also increased the dry weight of storage roots in 1988 and 1989 ($P = 0.01$ and 0.02, respectively) and the dry weight of shoots in 1988 and 1990 ($P = 0.01$ and 0.04, respectively).

DISCUSSION

Our work demonstrates the large effect of fibrous root infection on marketable yield of storage roots in the sweetpotato cultivar Jewel. There was a significant negative correlation between disease development on fibrous roots and yield of marketable storage roots in the field (Fig. 5). The severity of disease on fibrous roots was positively correlated with the percentage of diseased storage roots produced per plot and the number of diseased storage roots produced per plant (Table 3). In addition, the most important path of influence of disease on marketable yield was via the direct effect of the severity of disease on fibrous roots (Table 4). Reductions in yield were due in part to the effect of fibrous root disease on the number of storage roots produced per plant because these two variables were negatively correlated. Others have demonstrated a significant negative relationship between the "pox index" or severity of disease on storage roots and yield in naturally infested fields (17), but the relationship between yield and disease on fibrous roots was not demonstrated in previous work. Our data indicate a stronger correlation between disease on fibrous roots and marketable yield than between disease on storage roots and marketable yield.

Because the severity of disease on fibrous roots and marketable yield were negatively correlated, management strategies targeted at reductions in disease on fibrous roots should result in increased yields. Fumigation had the greatest effect on fibrous root infection in our work and increased the number and dry weight of storage roots produced per plant. In 1988, only fumigation significantly reduced disease on storage roots in fields with natural inoculum of *S. ipomoea* and, in 1988 and 1990, fumigation increased marketable yield. Levels of disease on both storage roots and fibrous roots were lower in 1989 than in other years, which may explain the lack of a fumigation effect on yield in that year. Soil pH in nonsulfur-treated plots in 1989 was below 5.2 for a time and may have been suppressive to disease (Table 2). Fumigation reduced disease on fibrous roots to a greater extent than either irrigation or sulfur alone, and the combination of treatments did not enhance disease control.

Drip irrigation of sweetpotato reduced the severity of Streptomyces soil rot on fibrous roots in all years, and, in the low rainfall field in 1990, irrigation reduced the number of diseased storage roots produced per plant (Table 1). Soil water contents were lower in nonirrigated plots in 1990 than in other years because less total rainfall occurred during the season. The reduction in disease severity on fibrous roots due to irrigation was equivalent to the reduction in disease due to soil treatment with sulfur, but it was not as large as the reduction in disease due to fumigation. Increased fibrous root growth in irrigated plots may have contributed to lower disease severity ratings, but increased dry weights of fibrous roots with irrigation were not observed in nonfumigated plots where the largest reductions in disease occurred. Growth of *Streptomyces* species is greatly reduced in water-filled soil pores (1,16,39). Reductions in the growth of *S. ipomoea* in soil and reductions in numbers of infections may be responsible for the reduced severity of disease on fibrous roots and storage roots in irrigated soils. Sweetpotatoes traditionally are not irrigated when grown on sandy soils in North Carolina. Although sweetpotatoes can survive drought, yield generally is compromised (9).

Sweetpotatoes respond positively to irrigations in dry years (3,10,29), but under waterlogged conditions low soil aeration may inhibit storage root formation (13). Irrigation increased the number but not the dry weight of storage roots produced per plant. In our work, irrigation did not reduce the severity of disease on fibrous roots or storage roots to a level large enough to result in significant yield increases.

Our data indicates that treatment of soil with sulfur reduced disease on fibrous roots in the field in some years but also compromised yield. In 1988, soil pH was not reduced to a level that was suppressive to disease (<5.2) over the season (sulfur × time effect was not significant) (Table 2). However, in 1989 and 1990, the sulfur × time interaction was significant, and sulfur significantly reduced yields as compared with nontreated plots (Fig. 7). Poole (30) also reported that sulfur reduced disease but caused injury to sweetpotato when applied in the row at 400 lb/A. Lorbeer (17) found that sulfur reduced yields of sweetpotato when applied at 1,000 lb/A, and therefore recommended fall application of 400 lb/A of sulfur after treatment of soil with chloropicrin. In contrast, others have reported reduction in disease when sulfur was broadcast in soil 6 wk before planting at rates of 700 to 1,200 lb/A with little detrimental effect on yield (12,27). Growth of sweetpotato cultivars may differ at low soil pH values. In-the-row application of sulfur on sweetpotato cultivar Jewel may be more detrimental to yield than broadcast applications. The detrimental effect of low soil pH on yield and the cost of sulfur application makes this option undesirable for growers in North Carolina.

Disease on fibrous roots can have a large impact on the development of disease on storage roots and subsequent marketable yield in the highly susceptible cultivar Jewel in the field. Others have demonstrated that disease on fibrous roots in greenhouse assays was negatively correlated with the total but not the marketable yield of 15 different genotypes of sweetpotato (26). It has been proposed that sweetpotato breeding lines with higher rates of root growth may be more resistant to disease than plants with lower rates of root growth (4). However, a critical examination of disease effects on fibrous root growth in infested field soils with the genotypes of sweetpotato now available is needed. Increased root growth could enable the plant to contact more inoculum in the soil and thus increase disease. Future research to develop resistance to the pathogen should continue to include evaluations of both fibrous root resistance and storage root resistance, because ultimately yield increases and reductions in disease on storage roots may be determined by optimizing resistance in fibrous roots.

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